STRUCTURE AND RELATIONSHIP OF CINCINNATIAN CYRTOCERINA

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INTRODUCTION

None of the three species currently referred to the genus *Cyrtocerina* Billings have been subjected to more than a superficial morphological examination. The present work deals with the investigation of *Cyrtocerina madisonensis* (Miller) formerly regarded as the only representative of the genus in the Cincinnatian. The specimens which have been included under that name in the collection of the University of Cincinnati Museum, and which form the basis of this study, proved on examination to include four species, three of which were closely related and evidently typical of *Cyrtocerina*. The fourth species, externally homeomorphic with *Cyrtocerina*, is referred with question to *Wetherbyoceras* Foerste, though as pointed out below, it probably represents a separate but allied genus now in process of description on the basis of better preserved Chazyan material.

These taxonomic details completed, there remains the more fascinating problem of the structure and affinities of *Cyrtocerina* itself. The vestigial septal necks and the inflated connecting rings are features which at once proclaim the relationship of this genus with some of our earliest cephalopods, those previously placed by the writer (1941), in the Eurysiphonata of Teichert (1933). As these forms are still rather inadequately known, it is not possible to determine the relationship of *Cyrtocerina* very precisely. It differs from all other post-Canadian genera in internal structure, and is quite probably related to *Levisoceras* Foerste, a genus which has not as yet been studied as closely as is desirable for comparison with *Cyrtocerina*. Ulrich and Foerste (1933) have referred *Levisoceras* to the Diphragmida, a group of cephalopods found in the Gasconade and earlier strata, and characterized by diaphragms or tabulae which cross the cavity of the siphuncle. *Cyrtocerina* clearly possesses no such tabulae, but if *Levisoceras* is properly placed in the Diphragmida, as seems probable from the meagre published evidence, *Cyrtocerina* is the only post-Canadian genus which can be traced directly to that group of cephalopods.

I am indebted to Mr. Clifton Smith, student assistant in the University of Cincinnati Museum, for assistance in the preparation of photographs. The expense of illustrative materials as well as part of the cost of the plates has been met by the Faber Publication Fund of the University of Cincinnati Museum.

Cyrtocerina Billings

Genotype: *Cyrtocerina typica* Billings

Cyrtocerina Billings, 1865, Pal. Foss., Geol. Surv. Canada, p. 178.
Barrande, 1867, Syst. Sil. de centre de la Boheme, vol. 2, pt. 1, p. 451.
Hyatt, 1884, Boston Soc. Nat. Hist., Proc., vol. 22, p. 266.
Miller, 1889, N. Amer. Geol. Pal., p. 436.
Holm, 1892, Geol. Foren. Stockholm, Forh., vol. 14, pp. 126, 209.
Clarke, 1897, Geol. Minnesota, vol. 3, pt. 2, p. 774.
Hyatt, 1900, Zittel-Eastmann Textb. Paleont., vol. 1, 1st ed., p. 517. (Reprinted with different pagination in later editions.)
Foerste, 1924, Denison Univ. Bull., Sci. Lab., Jour., vol. 20, p. 198.
Foerste, 1925, *Ibid.*, vol. 21, p. 11.
Foerste, 1933, *Ibid.*, vol. 28, p. 138.

Conch a rapidly expanding short cyrtoceracone, the aperture uncontracted. Section compressed, the convex dorsal (antisiphonal) side frequently obscurely angulate. Sutures are straight and transverse. The siphuncle is located close to the concave side of the conch, generally assumed to be ventral in such cephalopods. The siphuncle itself expands rapidly, being conical in form. The septal necks are vestigial, the connecting rings thickened and more or less produced into the cavity of the siphuncle in each segment. Their complex structure is described in the morphological section of the present work. The aperture has not been observed. Coarse rugose lines of growth indicate that there is no hyponomic sinus developed.

Discussion.—The short rapidly expanding endogastric conch of this Ordovician genus is not closely similar to that of any contemporaneous form, but instead is similar to *Levisoceras* and perhaps also comparable to *Shelbyoceras* of the Upper Cambrian and Basal Ordovician. Those genera are regarded as possessing diaphragms crossing the cavity of the siphuncle. No post-Canadian genera are known which are strictly comparable. On the basis of the exterior alone, *Cyrtocerina* might be confused with immature fragments of *Diestoceras*, but study of the interior will at once show the difference, as *Diestoceras* is cyrtochoanitic and actinosiphonate. The species described below as *Wetherbyoceras? cyrtocerinoides* Flower, n. sp. is similar to *Cyrtocerina* in aspect, but this is also cyrtochoanitic. Both *Wetherbyoceras* and *Diestoceras* can be distinguished not only by the difference in the structure of the siphuncle, but also by the relatively deep camerae, even in small fragments of early parts of the conchs of any known representatives of these genera.

Billings erected *Cyrtocerina* for the reception of short rapidly expanding conchs which were characterized by a large siphuncle on the dorsal (concave) side of the shell. Besides the genotype, *C. typica*, from the Middle Ordovician of the Paquette Rapids of the Ottawa River, he included in it *Cyrtocerina mercurius* Billings (1865, p. 193, fig. 179) of the Quebec group. Miller and Faber (1894) referred to the genus a species previously described as *Tryblidium madisonense* Miller from the Hitz layer, of Whitewater age, at Madison, Indiana. Clarke (1897), added *Cyrtocerina schoolcrafti* from the Decorah formation of Black River age of Minnesota. Foerste (1925) separated *C. mercurius*, making it the type of the new genus *Levisoceras* which he states is "apparently holochoanoidal in structure" while *C. typica* "is distinctly an ellipochoanoidal species." This was written at a time when Foerste regarded all Canadian or older cephalopods as holochoanitic, a view which he abandoned upon further investigation. Ulrich and Foerste (1933, p. 289), later reported that the necks of *Levisoceras* were *aneuchoanitic*, that is, terminating at the margin of the siphuncle with only vestigial curvature apicad, and that the interior of the siphuncle contained diaphragms. Upon this basis they placed *Levisoceras* in the Diphragmida. As shown below, *Cyrtocerina* is now known to agree closely with *Levisoceras* both in the form of the septal neck and the general appearance of the connecting ring, but clearly it does not possess diaphragms.

Cyrtocerina differs from all other post-Canadian cephalopods in the rapidly expanding form of the shell, the compressed section, and the position of the siphuncle close against the concave side of the shell. There is as yet no good criterion to show whether the siphuncle is dorsal in position as Billings assumed in writing the original description of the genus, or whether the conch has been curved endogastrically, so that the concave side is ventral, as Foerste believed, I have, in the following descriptions, retained Foerste's orientation, though out of regard to current usage rather than out of any conviction on the matter. The lines of growth of the surface fail to show any evidence of a hyponomic sinus by which the venter may be determined. No specimens have been found yielding either the ventral conchial furrow or the dorsal septal furrow which may be regarded as reliable criteria of orientation. (Flower, 1939, pp. 13–16.)

Knowledge of the internal structure of *Cyrtocerina* is based exclusively upon the Cincinnatian species discussed below, notably upon *C. madisonensis* (Miller) and *C. modesta* Flower. While there is every reason to believe that the genotype is similarly constructed, the conditions under which it is preserved are not favorable for the study of structural details. *C. typica* is apparently a very rare species. It is known to the writer only from Billings' type, which is preserved in the collections of the Victoria Memorial Museum at Ottawa. This is an exceedingly fragile silicified specimen from which all matrix has been removed by careful etching.

In all essential features it agrees with the Richmond species insofar as they can be observed. The large conical siphuncle is close to the concave side of the conch. Its interior presents a faintly annulated appearance. In considering this form as ellipochoanitic, Foerste probably regarded the constrictions as representing the septal foramina. However, in the light of the structure of *C. madisonensis*, it seems much better to regard the constrictions as the connecting rings which are produced in an annular manner into the cavity of the siphuncle. Even should material of the genotype be available which was contained in matrix and suitable for sectioning, it is to be feared that little more could be learned. Shells in that limestone are extensively replaced by silica. While this makes possible the removal of remarkably perfect specimens by means of etching, it has so altered original shell structure that thin section study of the material is profitless, and often opaque sections fail to show structures clearly.

Cyrtocerina is unknown in strata older than the Black River. *C. schoolcrafti* Clarke occurs in the Decorah formation of Black River age in Minnesota. *C. typica*, of the Paquette Rapids, occurs in a limestone which was formerly regarded as Black River age. Kay, however, regards the beds as belonging to the Rockland, lower Trenton, though his reasons for doing so have not been published. The genus is unknown in strata of higher Trenton or Covington age, and reappears only in the Whitewater formation near the top of the Richmond of Indiana. The three Richmond species, *C. madisonensis* (Miller) *C. patella* Flower and *C. modesta* Flower are best developed in the "Hitz layer," the southward thinning edge of the Upper Whitewater strata just above the Saluda beds at Madison, Indiana. One specimen was collected by the writer in the Whitewater strata at Versailles, Indiana. No representatives of the genus are known occurring either farther north or east.

This distribution suggests that *Cyrtocerina* belongs to that group of genera which appeared in eastern North America in Middle Ordovician time, then disappeared, presumably to arctic waters, to reappear in the east only near the close of the Richmond. The genus has not yet, however, been found in any of the strata laid down within the Late Ordovician Arctic embayment.

Cyrtocerina madisonensis (Miller)

(Pl. 1, figs. 3–4, 12–14; pl. 2, figs. 1, 3–7, 9.)

Tryblidium madisonense Miller, 1894 (adv. sheets, 1892) 18th Rep. Indiana Dept. Geol. Nat. Res., p. 318, pl. 9, fig. 38.
Cyrtocerina madisonense Miller and Faber, 1894, Cincinnati Soc. Nat. Hist., Jour., vol. **17**, p. **32**.

Original description.—"Shell medium size; apex high and almost straight above the anterior line of the shell; the shell slopes from the apex and arches a little toward the posterior part of the shell, but laterally and in front it descends abruptly to the margin; transverse section ovate; surface marked with fine, close, concentric lines and a few coarser ones, all of which appear to indicate lines of growth, instead of surface ornamentation; internal scars unknown.

The high apex and anterior portion of it seem to distinguish this species.

Found by J. F. Hammell, in the Hudson River Group, at Madison, Indiana, and now in his collection."

As can be seen, the *Cyrtocerina* was at first described in terms of a *Tryblidium*, a not unnatural error in dealing with a specimen of this peculiar cephalopod genus which failed to show any trace of the phragmocone. However, subsequent specimens showing the phragmocone caused Miller and Faber to revise the original description. Their revised description is quoted, as upon it depends the problem as to the exact identity of *Cyrtocerina madisonensis:*

"At the time one of the authors described, for the Eighteenth Indiana Report (Adv. Sheets Eighteenth Rep. Geo. Sur. Ind., p. 64) a fossil under the name of *Tryblidium madisonense* the internal part of it was not disclosed by the specimen at hand, while the external shell was remarkably well preserved and looked like that of a gastropod, and the form was that of a rather high Tryblidium. There was nothing in the shape or external appearance that would create the slightest suspicion that it belonged to the Cephalopoda. After that time specimens were collected showing a short, very rapidly tapering siphuncle, terminating on the concave side, below the apex and occupying the same position as the siphuncle in Cyrtocerina. Prof. Geo. C. Hubbard was the first to find that it was a chambered shell and possessed a siphuncle, and an examination of his specimens by the author led him to the conclusion that it is a true Cyrtocerina. The chambers are short, though longer than they are in *Cyrtocerina typica*, and the shell expands somewhat more rapidly than it does in that species.

"Heretofore there have been only two species known in this genus. The oldest, *Cyrtocerina mercurius*, from the Taconic rocks, the most elongated species and having the shorter septa, and *Cyrtocerina typica*, from the Black River Group. The species here under consideration is from the extreme upper part of the Hudson River group, which gives a range to this genus, commencing below the Silurian rocks and extending to the very top of the Silurian system."

Previously only this one Cincinnatian species of *Cyrtocerina* has been recognized, a species which marks the upper Whitewater beds above the Saluda, and is typically known from Madison, Indiana, though I have collected it as far north as Versailles, Indiana. Examination of the specimens that had been included under this name revealed that two genera were involved. One of these was characterized by the conical siphuncle noted in the description of Miller and Faber, and agrees closely with the original and revised descriptions. It was evident then, that *C. madisonensis* was among those forms which possessed a siphuncle similar to that of the genotype of *Cyrtocerina*. However, even among these specimens three distinct groups were recognizable on the basis of section and rate of expansion of the shell. Had there been but two, I should have been tempted perhaps to regard them as sexual dimorphism within a single species. However the three forms are sufficiently distinct to describe them as distinct species. The problem then arose as to which of these is identical with the original of *Cyrtocerina madisonense*, the type of which I was not able to locate. Fortunately the original description and figure furnish data by which this matter can be settled beyond any reasonable doubt. The ventral (siphonal) side of the conch must be straight or nearly so; the antisiphonal side must be curved, the curvature increasing as the aperture is approached. On this basis it is quite simple to select among the three species the one which was almost certainly the original of *C. madisonensis*. *C. patella* is a much larger form and one which expands more rapidly throughout. *C. modesta* is a much more slender form in which the curvature of the antisiphonal side is nearly uniform throughout, and in which the section is not nearly as compressed as in either of the other two associated species.

Revised description.—Conch rapidly expanding, compressed in section, the dorsal (antisiphonal) side faintly convex in the early portion, later becoming more curved, so that the rate of expansion decreases orad. The ventral (siphonal) side is nearly straight, probably slightly concave in the extreme apical portion, and becomes very faintly convex as the gerontic camerae are approached. The best preserved of our specimens has an initial height of 4 mm., expands to 25 mm., in the basal 12 mm., beyond which the increasing convexity of the siphonal side reduces the rate of expansion. At a height of 29 mm. the shell has a width of 25 mm. The lateral outlines are slightly convex; the section is compressed with the antisiphonal side the narrower of the two, obscurely angulate, and ridged when viewed adaipcally. The living chamber is very imperfectly known.

The septa are very closely spaced throughout the conch, the sutures tend to slope orad on the antisiphonal side as the aperture is approached. The siphuncle is conical, 1 mm. in diameter where the shell height is 10 mm; and 8 mm. at a shell height of 36 mm. The siphuncular structure is described in detail in another section of this paper.

Types.—Hypotypes, University of Cincinnati Museum, nos. 23965, 23966.

Occurrence.—From the Hitz layer of the Whitewater formation of the Richmond, from Madison, Indiana.

Cyrtocerina patella Flower, n. sp.

(Pl. 1, figs. 1, 5, 8.)

This shell is very rapidly expanding initially, and the convexity of the antisiphonal side increases only slightly, and at a much later stage than in *C. madisonense*. The conch expands in the basal 11 mm. to 24 mm. and 21 mm., the venter (siphonal side) straight, the dorsum only faintly convex, and the lateral outlines straight and rapidly diverging. A second specimen, consisting of a portion of a mature living chamber and gerontic camerae expands from 22 mm. and 25 mm. to a width of 40 mm. and an estimated height of from 45 mm. to 48 mm. in a length of 23 mm. The aperture is not preserved.

The phragmocone shows no features strikingly different from those of the above species. The camerae are exceedingly closely spaced gerontically, eight or nine occurring in the last 5 mm. of the siphuncle. The siphuncle is conical, close to the concave side of the shell. At conchial diameters of 22 mm. and 25 mm. it is 4.8 mm. wide and 5.2 mm. high.

Types.—University of Cincinnati Museum, Holotype, No. 23967, paratypes, No. 2638, 23968, 23969.

Occurrence.—The holotype is from the upper beds of the Whitewater formation from the road cut just east of the limits of Versailles, Indiana. The paratypes are from Madison, Indiana.

Cyrtocerina modesta Flower, n. sp.

(Pl. 1, figs. 2, 6–7; Pl. 2, figs. 2, 8.)

This species differs from the associated *C. patella* and *C. madisonensis* by its much more slender form and broader section. The ventral side is obscurely flattened, the dorsum obscurely ridged. The dorsal profile is slightly and evenly convex throughout, the venter is slightly convex, though nearly straight. The conch increases to a width of 22 mm. and a height of 24 mm. at a distance of about 23 mm. from the apex. At comparable distances from the initial point, both other species have sections both higher and broader. The lateral outlines are slightly and uniformly convex like those of the dorsum and venter. The siphuncle is close to the venter. The camerae are possibly slightly deeper than those of the other species. The form of the conch is best recognized from the accompanying illustrations.

Discussion.—The three specimens upon which this species is based vary somewhat in proportions, owing largely and perhaps entirely to distortion. One specimen is slightly compressed by pressure, but slightly obliquely compressed, so that the tip of the siphuncle is exposed by weathering on one lateral surface.

Types.—University of Cincinnati, No. 17170, holotype; No. 23970–71, paratypes.

Occurrence.—From the Hitz layer of the Whitewater formation, Madison, Indiana.

Wetherbyoceras? cyrtocerinoides Flower, n. sp.

(Pl. 1, figs. 9–11.)

Associated with the species of *Cyrtocerina* described above, is a small portion of a phragmocone which resembles members of that genus very closely in rapid expansion, the apparent endogastric position of the siphuncle, and the development of a compressed antisiphonal side. Nevertheless, sections revealed that the siphuncle was cyrtochoanitic, and that this specimen represents a hitherto unrecognized species. Probably also it represents an undescribed genus, though one which is known to the writer from other material, and is related to *Wetherbyoceras* Foerste, to which I tentatively refer this form.

The conch is compressed initially, with dorsum and venter equally rounded, with a hieght of 21 mm. and a width of 16 mm. In a siphonal length of 16 mm. and an antisiphonal length of 18 mm., the conch increases to a height of 33 mm. and a width of 29 mm. The greatest width of the shell is attained ventrad of the center of the section, and the dorsal (antisiphonal) side is much narrower than the siphonal side. All profiles of the conch are straight. The antisiphonal side is more strongly inclined from the line normal to the plane of the septa than is the siphonal side, giving the shell an endogastric aspect.

Five camerae and part of a sixth are preserved. The septa are shallow, the sutures apparently straight and transverse. The marginal siphuncle is crytochoanitic, the segments broadly expanded, rounded, strongly assymetrical vertically, as in many cephalopods with marginal siphuncles. The apical end of the connecting ring is broadly adnate to the septum on the ventral side, but free dorsally. At the adoral end of the segment, expansion is more marked on the dorsal than on the ventral side, but the brims are short and free on both sides. Small annulosiphonate deposits are found within the siphuncle. No trace of actinosiphonate structure is shown on this specimen. The surface of the shell is unknown.

Discussion.—This fragmentary specimen is very similar in aspect to one which Foerste figured and described as *Ooceras?* sp. from the Whitehead formation of Gaspé (Foerste, 1936, p. 381, Pl. 56, fig. 9.) The two species are almost certainly congeneric. Foerste remarked upon the similarity of his form with *Ooceras seelyi* and *O. lativentrum* as figured by Ruedemann (1906, pp. 496–499, Pl. 38, fig. 7–9). These species form the nucleus of a considerable group of Chazyan species for which a new generic name will be proposed at another time. These cephalopods are characterized by organic deposits within the siphuncle which may be apparently annulosiphonate in small or immature individuals. Some species never pass beyond the annulosiphonate stage, but large species finally attain deposits which are actinosiphonate and strongly reminiscent of *Minganoceras* Foerste (1938, pp. 104–5, Pl. 24, fig. 1–4). This genus appears again in the Platteville limestone, but does not appear again in the American section until found in the Whitewater formation of Indiana and the Whitehead formation of Gaspé. However, subsequent study of the little known genus *Wetherbyoceras*, the living chamber of which is still unknown, has shown that that genus is closely related to this one, so I tentatively refer the species to that genus. This does not, however, imply that *W? cyrtocerinoides* is at all closely related to either *W. valandighami* or *W. conoidale*, which are Covington species. The peculiar type of preservation of the deposits noted by Foerste in his species and in the Chazyan forms also, is not as startlingly displayed in the Cincinnatian species. There is, however, some indication of this mode of preservation in our specimen, which is not confined to the genus, but is widespread among fundamentally actinosiphonate cephalopods and has been noted by the writer in *Diestoceras*, *Cyrtacleistoceras*, *Minganoceras*, and *Archiacoceras*.

Type.—Holotype, University of Cincinnati Museum, No. 23971.

Occurrence.—Hitz layer, Upper Whitewater, Richmond group. From Madison, Indiana.

STRUCTURE OF THE SIPHUNCLE OF CYRTOCERINA

Opaque sections (Pl. 1, fig. 13, pl. 2, fig. 5) show that the siphuncle expands rapidly within the conch, taking on a conical form. The septal necks appear to be very short or wanting, and the interior of the siphuncle appears to be lined with an annular deposit. This differs from the usual annulosiphonate deposits in that the cavity of the siphuncle is constricted at the middle of each segment of the siphuncle, whereas normal annulosiphonate structure causes the constrictions to be located at the level of the septal foramina.

The same specimen in thin section (Pl. 1, fig. 12, 14; Pl. 2, fig. 1, 3, 4, 6, 7, 9) shows that the structure is quite unlike that of any known contemporaneous cephalopod. The septa are properly aneuchoanitic, that is, they terminate at the

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EXPLANATION OF PLATE I

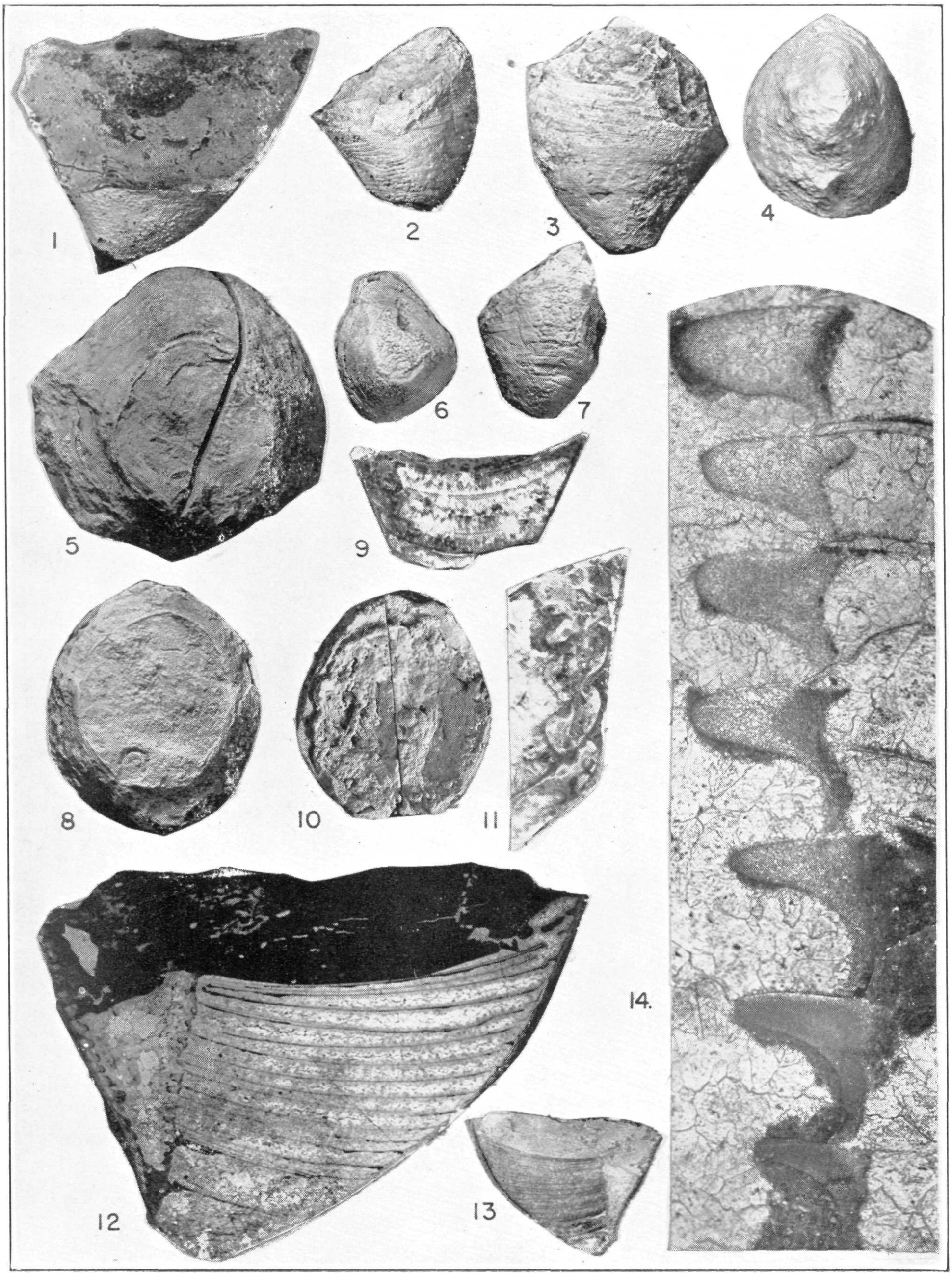
Cyrtocerina patella, Flower, n. sp. (1) Composite specimen showing vertical section of holotype (No. 23967) adorally, and unsectioned paratype adapically (No. 2368). (5) adapical view of holotype. (8) adapical view of paratype, No. 23968. Upper Whitewater formation. Holotype from Versailles, Indiana, other specimens from Madison, Indiana.

Cyrtocerina modesta Flower, n. sp. Paratype, No. 23970, Upper Whitewater formation, Madison, Indiana. Lateral (2), adapical (6), and dorsal (7) aspects.

Cyrtocerina madisonensis (Miller) lateral (3) and adapical (4) views of hypotype No. 23966. Madison, Indiana.

Wetherbyoceras? cyrtocerinoides Flower, n. sp. (9) vertical section, (10) adoral view, and (11) enlargement of siphuncle showing annulosiphonate deposits, of holotype, No. 23971. Upper Whitewater, Madison, Indiana.

Cyrtocerina madisonensis (Miller). Hypotype, No. 23965. (12) thin section, $\times 2\frac{1}{2}$; (13), opaque section of the same specimen, $\times 1$; (14), enlargement of dorsal wall of siphuncle from middle part of specimen, about $\times 18$.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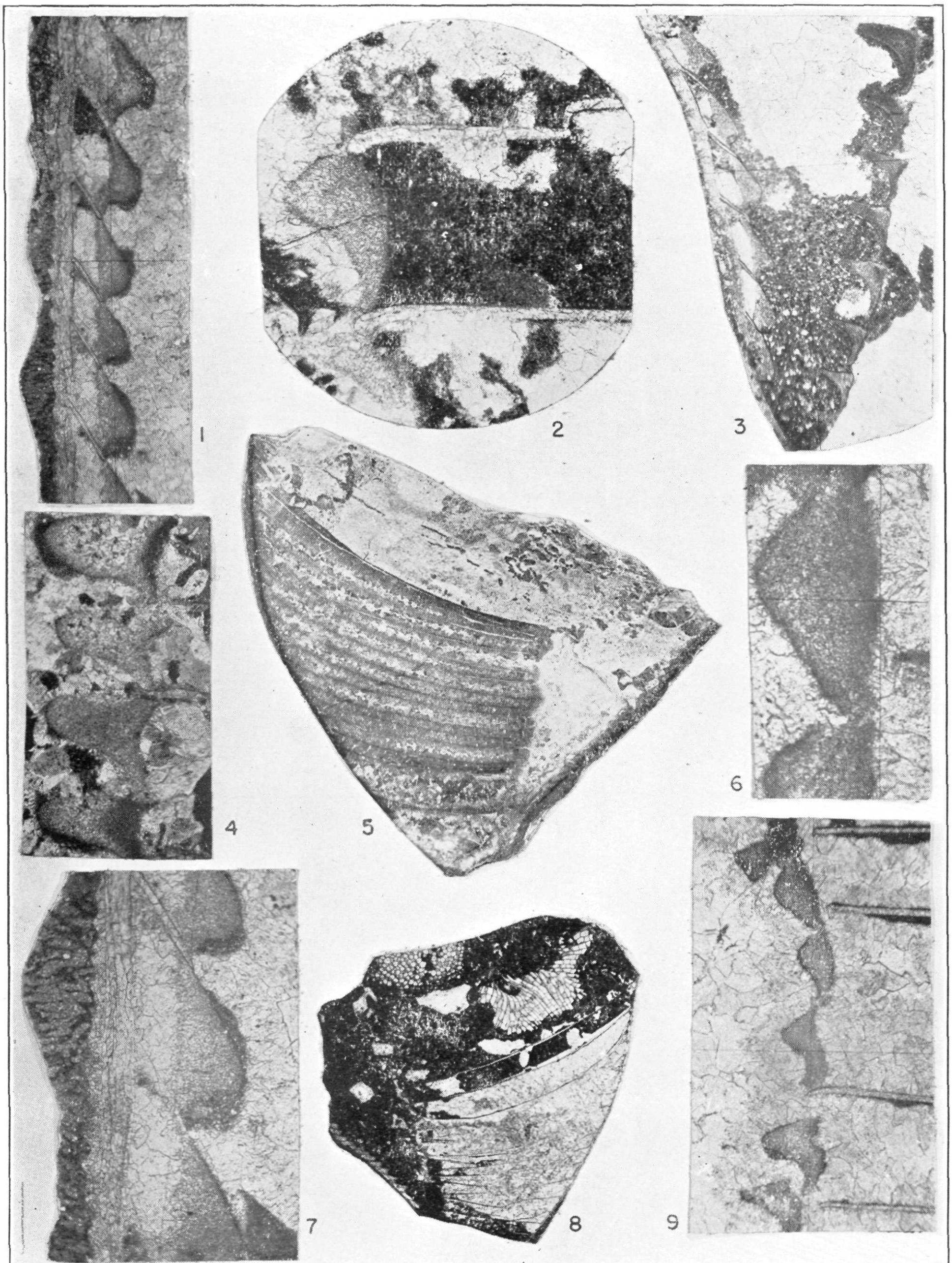
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margin of the siphuncle either without bending apicad at all, (Pl. 1, fig. 14, pl. 2, fig. 4, also figs. 1 and 7) or else there is only a vestige of a neck (Pl. 2, fig. 2). The structures which appeared in opaque section to represent accessory deposits, are revealed as curiously thickened connecting rings, rather variable in shape and composition, which are more or less produced into the cavity of the siphuncle. Both the thickness of the rings and the tendency for different regions to show structural variations, are reminiscent of the structures previously reported by the writer (Flower, 1941), as characterizing the older and more generalized of the Eurysophonata.

As structures and forms of the connecting rings vary somewhat from dorsum to venter, the two sides of the siphuncle are best discussed separately. The ventral side of the siphuncle is shown in Pl. 2, fig. 1, and a further enlargement of the apical portion of this figure is illustrated in Pl. 2, fig. 7. Traces of the mural part of the septum can sometimes be made out against the wall of the conch, but it is rarely possible to determine whether it extends forward for the entire length of the camera or not. The free part of the septum is straight, strongly inclined apicad, and terminates without any modification which could be construed as a true neck. The upper of the two septa shown in Pl. 2, fig. 7 is retouched to bring out its outline. The other is unmodified from the original.

The connecting rings are more or less semi-oval, the siphonal side convex, while the cameral side is usually straight, though, as seen in the uppermost segment of Pl. 2, fig. 1, it may occasionally be concave. The ring is divisible into two parts. On the siphonal surface one part appears as a thin dark band, sometimes more or less irregularly swollen in places. This contrasts strongly with the broader lighter area on the cameral surface. The condition is superficially similar to that noted in the aneuchoanitic *Proterocameroceras* (Flower, 1941, Pl. 1, figs. 3–5), but closer inspection shows that while zones of similar proportion occur in *Proterocameroceras* the contact between them is sharp. Here it is gradational.

The entire connecting ring contrasts strongly with the septa, the wall of the shell, or infiltrated calcite occupying the cavities of the camerae or siphuncle, in its fine grained texture. Examination of the connecting ring under high power shows that it is made up of very minute granules, probably crystals of calcite. If one traces the fine structure from a light to a dark portion of the ring it will be seen that the opacity of the siphonal surface is due to the presence there of closely packed minute granules, while in the lighter areas the grains are larger. The difference in appearance of the two regions is due to texture, and not to any pigment. The dark siphonal margin is very similar in appearance to the matrix within which the shell was buried, and in portions where the connecting ring is in

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EXPLANATION OF PLATE II

Cyrtocerina madisonensis, No. 23965. (1) Dorsal wall of siphuncle, septa and shell wall, about ×8, showing variation in form and appearance of connecting ring. (3) Adapical portion of section, showing invasion of matrix from broken apex of siphuncle, and modification of replacement of connecting rings in contact with matrix. ×8. (4) Dorsal wall of siphuncle, ×10, crossed nicols. Note coarse crystaline matrix and fine crystaline granules of connecting rings. Coarse crystals are seen in the second ring from the top only, evidently an alteration phenomenon. (5) Opaque section of same specimen, about ×2½. (6) Adoral dorsal connecting rings, about ×35, showing gradation of size of granules between light and dark areas. (7) Enlargement, about ×26, of dorsal wall of siphuncle, the adapical, portion of fig. 1. The outline of the upper septal neck is retouched. (9) Adoral dorsal siphuncular segments showing different form of segments, and distortion of conch, whereby a neck is apparently developed on the second septum from the top of the figure.

Cyrtocerina modesta Flower, n. sp. Holotype, No. 17170, Upper Whitewater, Madison, Indiana. (2) Adoral segment of dorsal wall of siphuncle showing form of ring, unusually well bent neck, and an abnormal bend in the septum in the upper right side of the photograph, ×22. (8) Vertical section complete, × 2½.

contact with matrix, it is very difficult to determine the boundary between the dark siphonal margin and the fine grained faintly dolomitic lime mud. This is shown, though somewhat obscurely, in Pl. 2, fig. 3, which shows the apical end of the siphuncle of our specimen. The extreme tip is missing, and matrix has entered through the broken end. However, the organic nature of the siphonal lining is shown clearly in more adoral segments, for it is well developed there in regions where matrix never penetrated. Quite probably this shell was buried at a time when some tissue still occupied the siphuncle. Matrix is present in the living chamber and has entered a little way into the siphuncle from either end. The greater part of the cavity of the siphuncle is occupied by calcite which has a sharp contact with the invading mud. This is believed to be one example, of which several others have been noted, of calcite representing the position of tissue present at the time of burial of a cephalopod shell.

The textural modifications of the connecting ring were plainly original, and indicate probably the deposition of the connecting ring as fine calcite granules of crystaline nature. These have been less susceptible to replacement and alteration than have the originally aragonitic shell parts. However, they have suffered some alteration, as can be seen when they are viewed through crossed nicols. Under such conditions (Pl. 2, fig. 4), the majority of the connecting rings are seen to be made up of fine granules, each of which has its own optical orientation so that at one position no two adjacent crystals ordinarily attain extinction. This causes the connecting rings to stand out strikingly against the large and irregular calcite crystals of the septa and of the infiltrated calcite in the shell cavities. However, this figure shows a number of areas in which recrystallization has taken place, notably in the upper two connecting rings, so that the granules are replaced by large irregular crystals. No trace of this phenomenon can be seen in ordinary light however, and the original granular structure seems to hold throughout under such conditions. This can be seen by comparing Pl. 2, fig 4 with the upper four segments shown in greater enlargement in Pl. 1, fig. 14. These phenomena indicate that both zonation and the granular nature of the connecting ring were probably original.

The dorsal side of the siphuncle shows the septa terminating ordinarily with no trace of a neck, but instead of sloping apicad throughout their length, they are essentially straight and transverse. This is shown most clearly in Pl. 1, fig. 14, and Pl. 2, fig. 4. Near the adoral end of the specimen (Pl. 2, fig. 8) an interesting condition is shown in which very short necks appear to be developed by abrupt bending. This part of the shell is slightly distorted, and the connecting rings have been moved out of line, and shoved slightly apicad from their original positions. Possibly the same force has been responsible for the bending of the tips of the septa, for the structure is irregular and far from uniform.

The nearest approach to a neck is shown in the adoral septum of the holotype of *Cyrtocerina modesta* (Pl. 2, fig. 2). Here the neck is faintly recurved. However, this specimen shows an abrupt bend in the septum before the siphuncle is attained, shown in the upper right corner of our photograph, which has been observed nowhere else and is probably due to injury. It is possible that injury may have affected the general organization of the shell enough to produce a slightly greater bending at the tip of the septum as well, so it is not certain that this condition is normal.

The connecting rings on the dorsal side of the siphuncle are more or less triangular in shape. The most typical form is shown in a series taken from the middle of Pl. 1, fig. 12, shown in Pl. 1, fig. 14. The ring is subtriangular, the cameral side straight or faintly concave, the siphonal side strongly produced, and extending farthest into the siphuncle at its adoral end. Farther orad in the siphuncle of the same specimen, (Pl. 2, fig. 9), the rings do not project as far into the siphuncle, and the greatest width is near the middle of the ring rather than at its adoral end.

The comma shaped ring of *C. modesta* (Pl. 2, fig. 2) may be diagnostic of the species, but enough segments have not been seen in which the connecting rings were preserved to make this certain.

The series of segments shown in Pl. 1, fig. 14 show the maximum variation noted in texture and mode of preservation of the rings on the dorsal side of the siphuncle. The upper three figures show the most typical condition. As on the ventral side, the greater bulk of the ring is made up of light, transparent, relatively large granules. The siphonal border consists of a more opaque area, again resembling matrix where it is most completely developed. As before, the two areas intergrade. The cameral surface of the ring shows a similar marginal opaque area. The simplest condition, showing the most gradual change from the central light area to the dark margin, is shown in the second segment from the top of our figure. In this the marginal opaque areas have not attained as great a development as in neighboring segments. The fourth segment from the top shows a curious darkening of a very broad band along the cameral surface. The next few segments are uniformly dark, a condition which is believed to be due to alteration connected in some manner with the invasion of sediments to these segments, as shown in Pl. 2, fig. 3. Rather strangely, segments which occur farther apicad in this series and which are more completely surrounded by matrix, show less modification. The second segment from the bottom of the same figure is unique among the rings observed in *Cyrtocerina* in that its siphonal surface appears to be marked by a thin line which seems to represent a definite wall. This sets off the main mass of the connecting ring from an irregular band of dark material resembling matrix, which in this case it probably is.

Interpretation of the structural significance of the various bands of the connecting ring of *Cyrtocerina* is still uncertain. Evidently the modification was original, for the same phenomena can be recognized, though differently preserved, under different conditions of alteration and replacement. The granular nature of the ring is what one might reasonably expect to be more widely found among fossil nautiloids if, as has been reported of *Nautilus*, their connecting rings are composed of fine crystals of calcite in contrast to the prismatic aragonite of the shell proper. The marginal opaque zones are of uncertain interpretation. Superficially, these bear a strong resemblance to various structures previously observed by the writer in eurysiphonate cephalopods. The eyelet reported in the tip of the connecting ring of several genera, notably among the Tarphyceratidae and in *Vaginoceras oppletum* (Flower, 1941), shows the same very fine grained condition, and the same degree of opacity as do these marginal zones. Similar also is the "inner zone" of the connecting ring on the siphonal surface in *Eurystomites.* Occasionally this and related genera have shown a similar zone on the cameral surface, but it was so faint that I did not at the time regard it as an original structure. Likewise the inner zone of *Proterocameroceras* is similar, though in that genus the zone is clearly set off from the remainder of the deposit, more strongly so than in any other form observed. The irregularity of the opaque material which lies along both the siphonal and cameral surfaces of the deposits, and which can also be seen occasionally against the septa in the camerae, is perplexing largely because of its irregularity. The most logical interpretation seems to be that this may represent vestiges of organic matter derived from tissues present in the camerae and siphuncle at the time of the burial of the conch.

RELATIONSHIP OF CYRTOCERINA

Hyatt (1883) originally placed *Cyrtocerina* with the Holochoanoidea, but later (1900) removed it to the Schistochoanites. That group, now no longer recognized, also contained the genus *Conoceras* Bronn of which Hyatt regarded *Bathmoceras* Barrande as a synonym. *Conoceras* is still very poorly understood, but *Bath-*

moceras appears to be a valid genus in which, as was shown by Holm (1899) processes from the wall of the siphuncle project centrad and orad into the siphuncle. These structures Holm figured as thickened connecting rings. So strong is the resemblance between these rings in *Bathmoceras* and the annulosiphonate deposits of *Polydesmia*, that it appears reasonably certain that *Bathmoceras* is ancestral to the Actinoceroidea. Further examination of this hypothesis showed that if this connection was real, the rings of *Bathmoceras* must be relatively complex. Though no differentiation of structure was shown by Holm, who worked only from opaque sections, it became evident that somewhere in the actinoceroid line there must have occurred a differentiation of the generalized part of the connecting ring and that part which was finally modified to form annulosiphonate deposits. This differentiation was one of material, for even in *Polydesmia* the deposits appear as structures quite distinct from the generalized part of the connecting ring. To eliminate this difficulty, it was suggested that the eyelet was the origin of the greater part of the mass of the deposit of *Bathmoceras*, and that the structure grew orad, finally thickening and sending a lobate process into the cavity of the siphuncle.

The connecting ring of *Cyrtocerina* is not unlike that of *Bathmoceras* in form. On the basis of outline alone the two could be homologized. However, the zonal development of the ring in *Cyrtocerina* is such as to indicate that either the genus must have some other relationship, or else that the structure of *Bathmoceras* is quite different from what Holm's figures and the strong resemblance to *Polydesmia* suggest. Further discrepancies are found in the form of the shells of the two genera, one a slender orthoceracone, the other a short endogastric brevicone. The genera further differ in the condition of the septal neck, *Cyrtocerina* having no true neck developed, while the necks of *Bathmoceras* are long and sometimes show more than a suggestion of cyrtochoanitic structure.

The siphuncle wall of *Cyrtocerina* shows, in the thickness and zoning of the connecting ring, features which the writer has taken as diagnostic of the generalized Eurysiphonata (Flower, 1941). This group, believed to spring from the Plectronoceratidae, is characterized by a thickened connecting ring in which various types of differentiation occur. It was regarded as beginning with the development of the Ellesmeroceratidae, straight or curved conchs with thick rings, and no accessory internal structures. From this group were derived the straight Baltoceratidae and the coiled Tarphyceratidae. The Endoceroidea developed first by the addition of endocones. Later prolongation of the necks produced holochoanitic structure, but the connecting rings are retained at least in the more primitive holochoanitic genera, and still show eurysiphonate characteristics. The rings of all of these groups exhibit two different types of patterns. Where the septal neck is short there is a dense thin inner (siphonal) zone and a lighter (cameral) inner zone. Where the necks are well developed and enclose the connecting ring for a considerable distance, the tip of the ring is differentiated into a mass of dense material, not unlike the inner zone, which was termed the eyelet. Assuming the deposits of *Bathmoceras* were developed from the eyelet, which grew forward over the inner (siphonal) side of the remainder of the connecting ring, it was possible to see in that genus the forerunner of *Polydesmia*, and the origin of the Actinoceroidea in which the inflated eyelet was modified into an annulosiphonate deposit.

While *Cyrtocerina* shows eurysiphonate affinities, it cannot be placed in any of the groups previously noted as members of the Eurysiphonata. On the other hand, it shows some features in common with the Diphragmida, which are very poorly understood at the present time, but the available evidence suggests that they also show eurysiphonate features. Possibly the connection is to be found in the genus *Levisoceras*, now placed in the Diphragmidae by Ulrich and Foerste (1933, 1936), but based upon a species originally placed in *Cyrtocerina*.

Levisoceras Foerste was first proposed because it was believed that *Cyrtocerina mercurius* was holochoanitic, while the genotype of *Cyrtocerina* was regarded as ellipochoanitic. Later Ulrich and Foerste (1933, p. 289), came to the conclusion that instead of being holochoanitic, the septal necks were actually very short, and that the connecting rings were peculiar in structure. Their statements are quoted below:

"However, two occurrences among the Diphragmida suggest that their structure may not have been holochoanoidal but ellipochoanoidal, the latter term having been introduced by Hyatt for siphuncles in which the septal necks are short and must be supplemented by connecting rings in order to produce a continuous siphuncle. For instance, several specimens from the central mineral region of Texas, apparently referable to *Levisoceras*, not only show the transverse tabulae within the siphuncle, but also segments of the siphuncle which are composed of short septal necks and intermediate connecting rings. Both surfaces of the septal necks are sharply defined from the adjacent matrix but those of the connecting rings apparently diffuse rapidly into the latter so that no sharp line exists between the rings and the matrix. Moreover, the substance of the connecting rings is slightly lighter in color than that of the septal necks."

The same forms were those which showed vestigial necks, as shown by the following statement of Ulrich and Foerste from the same paper: "In the Texan Diphragmida here described the septa curve downward only slightly on approaching contact with the siphuncle, this downward curvature being too slight to merit the name *neck*. They certainly are not orthochoanitic and the term aneuchoanitic (without neck) is here proposed for structures of this type."

Cyrtocerina agrees strikingly with *Levisoceras* in form. The genera have been separated on the basis of supposed internal differences. From the above quotations it can be seen that the genera agree in the aneuchoanitic necks, and the description of the connecting rings of *Levisoceras* might be equally well applied to those of *Cyrtocerina*. The only remaining difference is that *Levisoceras* is reported as possessing diaphragms which cross the siphuncle.

Cyrtocerina is unique among its contemporaries in the wall of the siphuncle. Its relationship can be best explained as a derivative of *Levisoceras* which has lost the diaphragms. At the present time, it is not possible to point out any other structural difference between the two genera. It is interesting to note in this connection that one section of *Cyrtocerina* which fails to attain the center of the siphuncle, shows apparent diaphragms because the processes of the connecting rings continue unbroken across the siphuncle. This suggests that some, though evidently not all, of the structures which have been described as diaphragms may be derived from connecting rings. This is particularly applicable to the exceedingly vague structures which Kobayashi (1933) has called pseudodiaphragms, in *Multicameroceras* and *Sinoeremoceras*.

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